

Factors affecting the reproductive success of dominant male meerkats

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Abstract

Identifying traits that affect the reproductive success of individuals is fundamental for our understanding of evolutionary processes. In cooperative breeders, a dominant male typically restricts mating access to the dominant female for extended periods, resulting in pronounced variation in reproductive success among males. This may result in strong selection for traits that increase the likelihood of dominance acquisition, dominance retention and reproductive rates while dominant. However, despite considerable research on reproductive skew, few studies have explored the factors that influence these three processes among males in cooperative species. Here we use genetic, behavioural and demographic data to investigate the factors affecting reproductive success in dominant male meerkats (*Suricata suricatta*). Our data show that dominant males sire the majority of all offspring surviving to 1 year. A male's likelihood of becoming dominant is strongly influenced by age, but not by weight. Tenure length and reproductive rate, both important components of dominant male reproductive success, are largely affected by group size and composition, rather than individual traits. Dominant males in large groups have longer tenures, but after this effect is controlled, male tenure length also correlates negatively to the number of adult females in the group. Male reproductive rate also declines as the number of intra- and extra-group competitors increases. As the time spent in the dominant position and reproductive rate while dominant explain > 80% of the total variance in reproductive success, group composition thus has major implications for male reproductive success.

Keywords: demographic factors, dominance, group effects, reproductive skew, reproductive tenure, sexual selection, *Suricata suricatta*

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Introduction

Identifying traits that affect the reproductive success of individuals is critical for our understanding of phenotypic evolution. Attempts to identify such traits are dependent on accurate measures of reproductive success and typically require long-term observational and genetic data of individually known subjects. Several studies have investigated individual reproductive success with sufficient detail to enable meaningful analyses of traits affecting reproductive success [e.g. life history (Brommer *et al.* 2002; Blums & Clark 2004;

Clutton-Brock *et al.* 2004); behavioural (Bensch *et al.* 1998); morphological (Jensen *et al.* 2004), and genetic (Amos *et al.* 2001)]. However, few studies have identified the traits that are important for reproductive success in highly cooperative species and we know particularly little about factors affecting male reproductive success.

In cooperative breeders, where more than two individuals provide extensive care for the offspring, a dominant pair typically monopolizes reproductive output for extended periods, sometimes leading to pronounced individual variation in lifetime reproductive success in both sexes (e.g. Clutton-Brock 1998a; Koenig & Dickinson 2004). In such species, the critical importance of acquiring and retaining social dominance for maximizing lifetime reproductive success may result in strong selection for competitive traits

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that facilitate these processes. In addition, as nonbreeding helpers can have a strong influence on the reproductive output of dominant breeders, the size and composition of social groups might also be expected to have an important influence on the lifetime reproductive success of dominant breeders. However, while a substantial theoretical literature and the associated empirical tests of these models have advanced our understanding of the causes of variation in reproductive sharing across cooperative species (e.g. Vehrencamp 1983; Faulkes *et al.* 1997; Solomon & French 1997; Clutton-Brock 1998b; Field *et al.* 1998; Reeve *et al.* 1998; Clutton-Brock *et al.* 2001b; Cant & Reeve 2002; Haydock & Koenig 2003; Heinsohn & Legge 2003), our understanding of the key traits allowing individuals to maximize their lifetime reproductive success in such species remains poorly developed (but see O'Riain *et al.* 2000; Russell *et al.* 2003; Hodge *et al.* 2008). In this study, we address this shortfall in our understanding by investigating the individual traits and social factors that affect the key components of reproductive success in male meerkats (*Suricata suricatta*).

Meerkats, are small (< 1 kg) obligate cooperative breeders inhabiting dry areas of southern Africa (Clutton-Brock *et al.* 1999a, b). Group size may reach 50 individuals (mean 12.4 ± 8.4 , median 11.8) and typically comprises a dominant breeding pair and a host of subordinates, both mature and immature, who contribute to the cooperative rearing of litters (Clutton-Brock *et al.* 2001a, 2003, 2004). Adult males and females do not differ substantially in body weight, and both sexes are sexually mature at around 1 year of age, but rarely breed before they are at least 2 years old. Pups are generally born to the dominant pair (up to four litters per year with a mean litter size of 4.0 ± 1.3 , $N = 181$ litters), but subordinates of both sexes do breed occasionally, albeit at low rates due to reproductive suppression by the dominant female and a lack of unrelated breeding partners (O'Riain *et al.* 2000). Females can either inherit the dominant position in their natal group if the existing dominant female dies, or they can join a coalition of males and form a new group. Males never become dominant breeders in their natal group and either join a coalition of females and form a new group, or immigrate into an existing group that has no dominant male. There is no obvious dominance hierarchy among subordinates of either sex, and when a dominance vacancy arises, or a new group forms, group members compete intensely with same-sex individuals to gain the dominant breeding position. Subordinate adult males, both immigrant and natal, often leave their groups on temporary prospecting forays, for one to a few days at a time, in search of extra-group breeding and dispersal opportunities (Young *et al.* 2005). These males remain group members and continue to contribute to cooperative activities (albeit at rates reduced in proportion to their investment in prospecting; Young *et al.* 2005), until they disperse permanently. Female dispersal arises from temporary evictions from the group by the dom-

inant female, during which multiple evictees occasionally band together to form a small coalition and attempt to found a new group with a coalition of foreign prospecting males. While our understanding of reproductive conflict among female meerkats is now well developed (Clutton-Brock *et al.* 2001b; Young & Clutton-Brock 2006; Young *et al.* 2006), this study aims to advance our comparatively poor understanding of the factors affecting the outcome of reproductive competition among males.

In this study, we use 12 years of life-history data, behavioural observations and genetic data to examine the factors that influence reproductive success in male meerkats. We begin by confirming that dominants acquire the majority of male reproduction (as previously shown by Griffin *et al.* 2003). We then look at the factors that influence (i) the acquisition of dominance, (ii) retention of dominance (i.e. breeding tenure), and (iii) a male's ability to monopolize reproduction while dominant (i.e. the proportion of pups sired born to the dominant female). Finally, to quantify the relative importance of the factors affecting the reproductive success of dominant males, we partition the variation in dominant male reproductive success into three components: dominance tenure, reproductive rate, and offspring survival.

Methods

Study population and data collection

All data were collected from a habituated meerkat population at the Kuruman River Reserve (26°58'S, 21°49'E) in the southern Kalahari Desert, South Africa. In this population, demographic, morphological and behavioural data have been collected since 1993 by over 50 researchers and highly trained volunteers. All animals were individually identifiable by small haircuts or dye marks, maintained without the need for capture. Groups were visited on a near-daily basis, and on each visit, individual demographic events were recorded, such as births, deaths, immigration, evictions and whether males had conducted temporary prospecting forays. From these long-term records, data such as individual origin and age, group size and composition on a particular day and other variables could be extracted. Most individuals were habituated to step onto a portable electronic balance from a young age, allowing us to collect regular weights for over 95% of the study population. Weight data were collected prior to their morning foraging trips to reduce variation caused by variations in stomach content weight. More details about the study population and data collection can be found in (Russell *et al.* 2002). Meerkats were considered pups until the age of 3 months and adults when older than 12 months.

Dominant individuals were identified by their behaviour towards other group members (Griffin *et al.* 2003). Dominant males had enlarged anal glands and scent-marked more

frequently than other males, and asserted their dominance over other group members in a variety of ways, including anal marking, rubbing other individuals with their chin, or in extreme cases, by attacking and biting. Subordinate males respond to these dominance assertion behaviours by adopting a characteristic grovelling posture, usually accompanied by a peeping vocalization, and either grooming the dominant or rolling over onto their backs. Changes in dominance, often preceded by a short period (hours to days) of intense fighting, were accompanied by dramatic changes in behaviour in the contesting individuals, and hence were immediately recognizable. Males were only recorded as having assumed the dominant position if all other adult males in the group responded submissively to dominance assertion behaviours for at least 1 week.

Genetic methods

We obtained tissue samples for genetic analyses by cutting a small piece of tail-tip (~2 mm) with a pair of scissors from pups when they first emerged from the natal burrow at approximately 3 weeks of age. Only pups that emerged from the natal den could be sampled, but as previous studies have shown that offspring mortality prior to emergence is rare (Russell *et al.* 2002), it is likely that we sampled the majority of pups born into our study population. Tissue samples were also taken from adults that immigrated into the study population. All sampled individuals returned to what appeared to be undisturbed behaviour shortly after the sample was taken, none of the cuts developed any (visible) infections, and we have no evidence that the procedure had any long-term negative consequences. Samples were stored in DMSO or 100 mM EDTA 95% ethanol at -20 °C. We extracted DNA using standard chelex or phenol/chloroform methods (Maniatis *et al.* 1982) and stored samples in double-distilled water at -20 °C.

Fourteen microsatellite markers were used to assess paternity (see Table 1). To enable multiplexing, we changed the annealing sites of markers Ssu 7.1, Ssu 8.5, Ssu 11.12, Ssu 12.1, and Ssu 13.8 (Table 1). Touchdown 10 µL polymerase chain reactions (PCR) multiplexes contained three to four markers, labelled with fluorescent dyes HEX, TET and FAM (PE Applied Biosystems). All PCRs contained 1.5 µL Applied Biosystems Gold Buffer, 0.8 µL 25 mM MgCl₂, 1 µL 10 mM dNTP mix, 0.2 µL *Taq* Gold. The amount of marker used varied between markers and multiplexes (from 0.25 to 0.8 µL 10 mM marker, equivalent to 2.5–8 pM) and the annealing temperature ranged from 48 to 58 °C. Typical cycling conditions were 12 min at 95 °C, 20× (30 s at 95 °C, 30 s at 58 °C (-0.1 °C/cycle), 1 min at 72 °C), 15× (30 s at 95 °C, 30 s at 56 °C, 1 min at 72 °C), 10 min at 72 °C. PCR products were run on a PE Applied Biosystems ABI 377XL using TAMRA 500 as internal size standard and cellulose combs to prevent spill-over. Results were extracted and analysed

with GENOTYPER software. The entire procedure from DNA extraction to genotyping was performed in no particular sample order to avoid observer biases. Extracted lanes were compared to the raw gel image to eliminate false dye peaks.

Individual genotypes were compared to those of their relatives (where known from life-history data) to isolate genotyping errors and further improve the quality of the data. Since mother and siblings can reliably be identified from observational data (Griffin *et al.* 2003), it was possible to rectify some of the genotyping errors using simple logical rules based on Mendelian patterns of inheritance. In cases of single repeat errors (due to PCR stage misprint or variations in fragment mobility in gels), inferences from the genotypes of relatives sometimes allowed us to directly correct the genotype. Additionally, dropouts or poor amplification may cause false homozygotes. Wherever possible, we corrected such errors by looking at the raw gel to see if peaks just below the threshold had been omitted, or alternatively, from inferences made from the genotypes of relatives. However, sometimes no correction could be made objectively, despite an obvious error, so these false alleles were left unaltered. Duplicate runs showed an overall error rate of about 3%, of which the majority could be corrected. We therefore assumed an overall conservative error rate of 2% in the final genotypes.

Analyses are based on 792 individuals (82% of the population). Most loci showed moderate to high variation with up to 17 alleles and mean heterozygosity levels of 0.73 (Table 1). Three loci showed significant heterozygote excess and, overall, the population showed slightly higher-than-expected heterozygosity levels (paired $t = 3.62$, d.f. = 14, $P < 0.05$). After Bonferroni correction, only one marker deviated significantly from Hardy–Weinberg expectations, possibly because its low variation (with only three alleles) made it susceptible to random effects. Overall, levels of genetic variation adhere to what could be expected in a large population of kin groups exhibiting inbreeding avoidance and strong reproductive skew (Chesser 1991; Dobson *et al.* 1998). On average, we obtained data from 9.3 ± 3.1 loci per individual. The overall amplification success was $78\% \pm 18\%$ (mean \pm SD) and all individuals included in the analyses were scored for a minimum of five loci, although individuals at the lower end of the range (with five to eight loci amplified) could often not be assigned fathers with a high degree of confidence.

Paternity assignments

We assigned paternity using the software CERVUS (Marshall 2001). When more than one female gave birth simultaneously, we used genetic data when available to identify the mother by exclusion. Dates of birth could be determined to within 1 day and most individuals included in our analyses had known mothers (> 99%). Where maternity was unknown,

Table 1 Microsatellite statistics. Significance levels for Hardy–Weinberg equilibrium have not been Bonferroni-corrected. The annealing sites of markers Ssy 7.1, Ssu 8.5, Ssu 11.12, Ssu 12.1 and Ssu 13.8 were redesigned to allow multiplexing (changes within brackets)

Marker	Ref	Sequences 5'–3' (forward/reverse)	No. of individuals	No. of alleles	Size range	H_O	H_E	P value
AHT130	1	CCTCTCCTGGTAAGTGCTGC TGGAACTACTGGTCCCCAG	639	17	122–156	0.77	0.73	0.44
Fca 045	2	TGAAGAAAAGAATCAGGCTGTG GTATGAGCATCTCTGTGTTCTGTG	270	11	158–178	0.80	0.64	0.08
Fca 077	2	GGCACCTATAACTACCAGTGTGA ATCTCTGGGGAATAAATTTTGG	677	10	96–114	0.61	0.59	0.47
Fca 232	2	ATGACCATCTCAAACATTCATGG AGCTGAGTTTGCGTTTATCATG	714	12	90–118	0.62	0.64	0.36
HG 8.10	3	AATTTCTGAAGCAGCCCAAG GAATTTCTTTCTAGCATAGGTTG	263	10	190–225	0.76	0.63	0.18
*Ssu 7.1 (+18 bp)	4	ATCCCTTAATGCATAGGCACAC CCTGCTAGTCTTCTCCGTGCG	676	11	158–178	0.77	0.63	0.14
*Ssu 8.5 (+44 bp)	4	GTCAGGTGCTTAACTGACTGG TGGAGTCACTCATTTGGTTTGG	492	17	252–284	0.86	0.74	0.04
Ssu 10.4	4	CTCCAGTTCTTTTCCCTGGAG CATTGGGTGCACACTGTCTCC	674	17	108–140	0.79	0.73	0.35
*Ssu 11.12 (–11 bp)	4	CAGGAAATTTTCATCCTGGTAG AGCTTTATTTTCTCTGTGCA	689	14	102–128	0.75	0.69	0.40
*Ssu 12.1 (+26 bp)	4	TTGTTTAAAGCCACCCAGTCTG TCCTGGTGACACAAACAATGC	674	13	158–182	0.78	0.67	0.17
*Ss 13.8 (+69 bp)	4	GATCAGTGAGAACAGAAGTGC ACCTCCTCCTCCAGATGCATC	407	11	204–228	0.68	0.64	0.48
Ss 13.9	4	TGGAAGTAGGTAGAAGACATTT AGGGATGAGAAGACCACCCTC	200	3	130–134	0.66	0.25	0.00
Ss 14.14	4	GCATTAACCTATAATTTGCTGAG CCCGAGGACAGAGACAAAATG	219	9	111–127	0.80	0.62	0.02
Ssu 14.18	4	GATCACCTAAAATTTGCACTACT TCAACCTGCAGGTTTCAGACC	192	8	129–149	0.64	0.57	0.41
Average \pm SD			485 \pm 215	12 \pm 4		0.73 \pm 0.08	0.63 \pm 0.12	

1, Holmes *et al.* 1995.2, Menotti-Raymond *et al.* 1999.

3, Goodman 1997.

4, Griffin *et al.* 2001.

*modified annealing sites.

 H_O , observed heterozygosity. H_E , expected heterozygosity. P , probability.

we ran the analysis without this information, but loss of power resulted in few significant assignments. We included adult group males and all males seen prospecting at the group during a 2-week window around the calculated conception date as candidate fathers. Pregnancy lasts approximately 70 days; thus, conception could be back-calculated from known dates of birth (Clutton-Brock *et al.* 2001a). This gave a typical candidate file of about 10 males (range five to 50). To reduce false assignments, we excluded males who were offspring of the mother. Previous genetic work has shown zero prevalence of within-group incestuous matings (Griffin *et al.* 2003). Behavioural observations also strongly support this contention, e.g. if all immigrant males die, a natal male may become socially dominant in their natal

group (typically alongside their mother). These males do not mate guard, but instead conduct extraterritorial prospecting forays for dispersal and mating opportunities. Immigrant dominants, on the other hand, never conduct such extraterritorial forays (Young *et al.* 2007). These rare 'natal dominants' have been excluded from our analyses, and thus throughout, the term 'dominant male' refers to immigrant dominant males. Our CERVUS settings assumed we had genetic information from 95% of candidate fathers, accounted for missing data and an error rate of 2%, and finally, assumed that each assigned candidate had five related males (with an average relatedness of $r = 0.25$). We attempted to assign paternity to 658 pups. Individuals that were adults when first seen were omitted from paternity analysis as their

candidate fathers were not known. We assigned paternity with > 80% confidence for 528 individuals. Of these, a further 333 individuals could be assigned a father with > 95% confidence. This analysis will have been unable to assign paternity to fathers not included in the candidate file (e.g. foreign prospecting males not seen at our groups or those that were unsampled as they originated from outside the study population). This is expected to give rise to an underestimation in the prevalence of extra-group paternity, although it should not give rise to any consistent bias among the classes of male within the groups (e.g. dominant vs. subordinate) nor among the groups in our likelihood of assigning extra-group paternity. The majority of failed assignments appear to have been caused by insufficient genetic data (i.e. poor amplification), rather than a lack of the fathers in the candidate files. For a detailed study of the prevalence and causes of extra-group paternity in this population, see Young *et al.* (2007). When calculating the distribution of paternity among dominant and subordinate males, we only included assignments with probability of > 95%. This is because, as the dominant male sires the majority of offspring, false assignments caused by random error will inflate the number of pups sired by nondominant males. For our other analyses, the inclusion of paternity assignments at 80% confidence adds noise to the data, but will not introduce any systematic bias to the analyses.

Statistical analyses

Several analyses involved repeated measures of the same individual or group, and in these cases, generalized linear mixed models (GLMMs) were used. These are similar to generalized linear models (GLMs) except that GLMMs allow both fixed terms and random terms to be defined. If random terms (individual, litter and/or group) were not significant ($P > 0.05$) simple GLMs were used (Pinheiro & Bates 1996). In all cases, GLMMs (with random terms retained) and GLMs yielded qualitatively similar results. All two-way interactions were tested, but only presented if significant. Unless otherwise stated, means are presented with standard deviations (\pm SD). All statistical tests are two-tailed. Computations were performed in GENSTAT (VSN-International 2005), STATISTICA (StatSoft 2005), RELATEDNESS (Goodnight & Queller 1999), GENEPOP (Raymond & Rousset 1995), and Microsoft Excel (including the add-in POPTOOLS; Hood 2004). The data presented come from 67 completed dominance tenures by 54 males, in 23 social groups. Two males held two dominance tenures in the same group (regaining dominance within their group after losing it for a period). Seven males held two dominance tenures in different groups (dispersing into a new group to hold dominance after their first dominance tenure had ended). Two males held dominance tenures in three successive groups, and a further two males held two dominant tenures in one group, and a

third tenure in a second group. Some analyses did not require the completion of dominance (e.g. distribution of paternity within litters), and for these, we included data from open-ended tenures (i.e. with unknown ending dates), bringing the total up to 72 dominance tenures by 60 individuals. As all data were not available for all individuals, sample sizes vary between analyses. We only included males that held their dominance tenure for more than 3 months to avoid biasing our results with poor estimates of reproductive rates arising from short monitoring times (e.g. those males that did manage to sire a litter within their short 3-month tenure would be attributed an unrealistically high reproductive rate). This 3-month cut-off was applied to all analyses.

Acquisition of dominance

Estimating the proportion of individuals that acquire the dominant position in their lifetime can be difficult, since spatial restrictions of field studies often make it impossible to assess whether animals that disappear have died or successfully dispersed. However, if there are no qualitative differences in population dynamics between the observed population and that surrounding it, demographic data can be used to produce accurate estimates of these parameters (see Lucas *et al.* 1994). It follows logically from the assumption of demographic and spatial homogeneity that the fraction of animals disappearing will correspond to the number from which successful immigrants must emanate from. In other words, the number of animals disappearing will result in the same number of successful emigrants as there are successful immigrants. To obtain an estimate of the proportion of males that become dominant, we therefore divided the number of dominance acquisitions at our study site by the number of male pups that emerged. This gives an estimate of the likelihood that an emergent male pup has of becoming dominant during its lifetime. We excluded males that acquired a second dominance tenure in a new group. The same logical argument could, in principle, be applied to the temporal issue of which pups to include when calculating the proportion that became dominant during the sampling window. However, because the study area has continually been expanded, the number of groups under study has also increased. As a consequence, the end of the study interval holds more young individuals that have not yet reached an age where they realistically can compete for dominance. We therefore limited our analyses to individuals that were at least 4 years old at the end of the study period, an age where well over half of all dominant males have acquired their dominance tenure.

To investigate the factors that influenced dominance acquisition, we looked at male survival probabilities over time (assuming the surviving number of emigrating males equalled the number of surviving immigrants, see previous

paragraph for rationale) and calculated the proportion of males in each age category that acquired dominance. To establish at what age males become dominant, and to investigate the importance of age, we compared the age of the successful male in relation to other males within the group at the time of the dominance change. Finally, we investigated the effect of weight by comparing the weight of all males competing for dominance, as well as doing a separate comparison including only same aged males.

Factors affecting tenure length

To investigate the factors affecting tenure length, we log-transformed dominance tenure (days) and fitted it as the dependent variable in a GLM. The following explanatory terms were tested: age at dominance acquisition (days), weight at dominance acquisition (grams), mean group size (mean number of individuals older than 6 months), mean number of competitors (males unrelated to the dominant female who were older than 1 year) and mean number of unrelated females throughout the males tenure. We obtained mean values by recording the number of individuals in each category at the start of each 6-month period of dominance, and averaging these values over the dominance tenure. Mean group size was moderately correlated with the mean number of adult females in the group (adjusted $R^2 = 0.6$). Group size was not correlated to the mean number of males unrelated to the breeding male (adjusted $R^2 = 0.0$). Analyses were conducted on 67 complete dominance tenures.

Factors affecting the proportion of pups born in the group sired by the dominant male

To investigate the factors affecting the dominant male's reproductive share per litter, we included the number of pups per litter sired by the dominant male as the dependent variable in a GLM with a binomial error structure and complementary log-log link function. The total number of offspring typed in litter was included as the binomial denominator. This allowed us to investigate the proportion of offspring sired by the dominant within the litter, while weighting the data according to the number of offspring genotyped. The following explanatory terms were tested: dominant male age (days), dominant male weight (g), group size at conception (number of group members > 6 months), number of competitors at conception, number of prospectors seen at group in the 2 weeks around conception, the number of unrelated females in the group at conception, rainfall (mm), and time spent with current dominant partner. The analysis was conducted on 107 litters, born during the tenures of 26 dominant males in 14 groups for which we had comprehensive data. Only litters born to dominant

females were included. The dominance status of mothers could be easily determined through behavioural observations (Hodge *et al.* 2008).

Variance components of reproductive success while dominant

The reproductive output of dominant males will be a product of the length of time they hold the dominant position (tenure), the rate at which they produce offspring during their tenure (breeding rate) and the survival of any offspring they produce. To compare the relative importance of tenure, breeding rate and offspring survival on the reproductive output of dominant males, we conducted a multiple linear regression in which the total number of offspring produced that survived to 3 months was included as the dependent variable. Dominance tenure (number of months in the dominant position), breeding rate (number of offspring produced per month of tenure) and offspring survival (proportion of offspring produced that survived to 3 months) were included as explanatory terms. All were log-transformed to reduce the model to simple additive terms, which removes two-way interactions (see Clutton-Brock 1988). We used the standardized regression coefficients to compare the relative importance of each variable on the dependent variable, which effectively partitions the total variance in reproductive success into its three constituent components. This approach allowed us to identify which components had the biggest influence on male reproductive success. Analyses were based on 36 males for whom we had exhaustive data.

Results

Paternity distribution

Our results confirm the findings of an earlier study (Griffin *et al.* 2003) that dominant males sired the majority of offspring in the study population for which fathers could be assigned (~86%, or 286 of 333 pups assigned at 95% confidence). Intra-group subordinate males sired just over 4%, and the remaining 10% of pups were sired by extra-group males (Fig. 1). These numbers reflect the distribution of paternity among offspring of known paternity. Since we only included extra-group males as candidate fathers if they were actually seen at the group and were genotyped (i.e. from within our study population), this is expected to underestimate the proportion of young sired by extra-group males (for a detailed study of the prevalence and causes of extra-group paternity in this population, see Young *et al.* 2007).

When separating litters born to dominant and subordinate mothers, the patterns of paternity differ substantially. Of pups born to the dominant female ($N = 299$ assigned at 95%

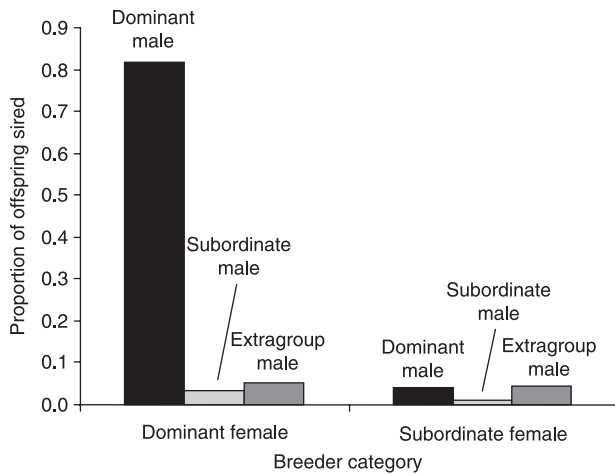


Fig. 1 Distribution of paternity of pups born to dominant and subordinate females. Only assignments with > 95% confidence ($N = 333$) were used when constructing the figure to minimize bias (see Methods).

confidence), dominant males sired 92%, subordinate males sired 4% and extra-group males 5%. On the other hand, subordinate female litters ($N = 34$ assigned at 95% confidence), which accounted for 10% of all pups born, were only sired by the dominant male in 43% of cases, and never when the subordinate female was his daughter. Subordinate males and extra-group males sired 10% and 47% of pups born to subordinate females, respectively (Fig. 1).

Dominance acquisition

Between 1993 and 2004, approximately 17% of males born or immigrated into our population became dominant at some stage during their life (35 out of 210) with great variation in tenure lengths (13.7 ± 15.0 months, median 9.8). Males acquired dominance at an average age of 39.6 ± 16.2 months ($N = 55$, range 12.7–81.3 months). Males below the age of 3 years had a low probability of acquiring the dominant position, whereas nearly all individuals reaching 8 years of age become dominant (Fig. 2). Relative age was a strong predictor for dominance acquisition when a vacancy arose (Fig. 3) and the oldest male acquired dominance in the majority of cases (60 of 72; $\chi^2 = 18.0$, d.f. = 1, $P < 0.001$), e.g. the two males in Fig. 3 that acquired dominance at 1 year of age were, despite their young age, the oldest males in their respective groups at the time.

The relative weights of males competing for dominance had no significant effect on the outcome. For competitors of different ages, there was no effect of weight on the likelihood of winning a fight [$t = 1.66$, d.f. = 42, $P = 0.10$; mean weight winner 713 ± 56 grams (median 720 grams), mean weight loser 735 ± 75 grams (median 734 grams)]. The same result was found when comparing males of identical age (paired $t = 0.10$, d.f. = 17, $P = 0.91$), although the differences between

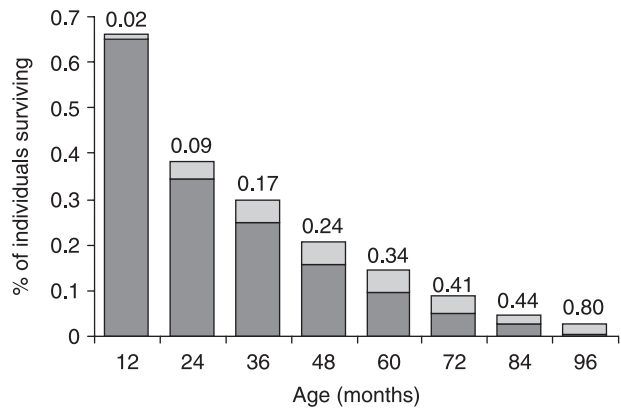


Fig. 2 Effects of survival on probability of attaining the dominant position (proportion of males surviving to 1, 2, 3 ... 8 years of age that acquired alpha status). The total height of the bar indicates the proportion of males that emerged from the den that survived to each age class (e.g. nearly 40% reach 2 years). The lighter grey area shows the proportion of individuals in each age class that were dominant (also shown in numbers above each figure). The figure is based on 197 individuals for whom complete life-histories were known.

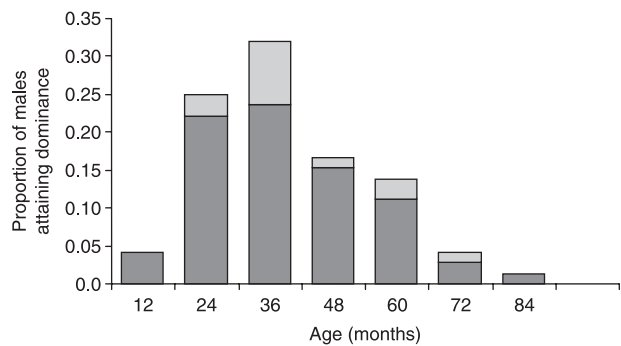


Fig. 3 Effect of age on the acquisition of alpha status in males ($N = 72$ dominant individuals). Total column height equals the proportion of males acquiring alpha status at different ages. Light grey areas show the proportion of cases where the individual acquired alpha status despite not being the oldest contender.

the winner and the loser ranged from -98 to 97 g (often > 10% of body weight) with a mean of -1.5 ± 59.5 g (mean weight winner 720 ± 66 grams (median 727 grams), mean weight loser 721 ± 81 grams (median 700 grams)).

Factors affecting tenure length

Dominant male tenures were longer when the average group size across their tenure was large, but shorter in groups that held a larger number of adult females unrelated to the dominant male (Table 2). Neither dominant male age, weight, nor the dominant female's age at male dominance acquisition had any significant effect on tenure length. Including all tenures with known start and end dates means male tenure length was 14.3 ± 15.8 months ($N = 67$ by 54

Table 2 Factors affecting tenure length (in days), based on 65 dominance tenures

Variable	Estimate	SE	d.f.	P value	Comment
Mean no. of unrelated females to dominant male in group	-0.15	0.03	56	< 0.001	Females > 1 year at start of each 6-month window averaged
Mean group size	0.06	0.02	56	< 0.001	Individuals > six months at start of each 6-month window averaged
Male age (days)	-0.04	0.13	54	0.76	At acquisition
Male weight (g)	0.00	0.00	33	0.10	Mean weight during the 30 days preceding conception
Mean no. of male competitors	0.03	0.03	56	0.32	Males > 1 year at start of each 6-month window averaged
Constant	2.34	0.13	56	< 0.001	

Results from a general linear model with tenure logged as the dependent variable and a normal error structure and identity link function. Individual was not significant as a random term and was dropped from the analysis ($P > 0.05$).

individual males, median = 10 months, range 0–68 months). Of these, 39 ended when the male was ousted by another male, 13 because the male died, and 15 because the dominant female died, which typically led to the male dispersing soon afterwards.

Dominant males were only noted to willingly depart their groups once all females to whom they were unrelated had either died or dispersed, and so their pursuit of a second tenure elsewhere appears to be driven simply by the need for access to unrelated breeding partners (i.e. not by a drive to control a larger group of females, as has been reported in lions, *Panthera leo*; Packer & Pusey 1993). For males with sequential dominance tenures, there was no significant difference in group size or number of females between the first and second tenure. Males assuming a second tenure ($N = 15$ cases) experienced a mean decrease in group size of 2.4 ± 10.2 individuals and a mean decrease in the number of females to whom they were unrelated of 1.7 ± 9.7 females (in both cases, paired t -tests revealed $P > 0.4$).

Factors affecting the proportion of pups in the group sired by the dominant male

In litters where all pups had fathers assigned at 95% confidence, about 17% of litters had multiple fathers. Because our mean number of genotyped pups per litter is 3.1, the chance of a false assignment becomes $1 - 0.95^{3.1}$ or 14%. This makes it precarious to estimate the true frequency of multiple paternity. But although we have included assignments as low as 80% confidence to maximize our sample size when investigating factors affecting reproductive success, it is important to realize that although such a relaxed assignment introduces some noise in the data set, it does not bias the data. Our results here show that the proportion of pups in each litter that were fathered by the dominant male decreased with increasing numbers of competitors in the group and with increasing numbers of prospecting males

seen at the group during the litter's conception window (Table 3). After controlling for these effects, dominant males sired a higher proportion of the dominant female's litter when they were in larger groups. Weight, age, rainfall, number of unrelated females or time spent with the dominant partner, had no significant effects on the dominant male's reproductive share per litter (Table 3).

Variance components of reproductive success while dominant

Our measure of dominant male reproductive success varied from zero (one male) to 60 during one or multiple tenures (10 ± 12 , $N = 40$). The largest components of variance in dominant male reproductive success were time spent in the dominant position (41.0%; Table 4 and Fig. 4) and the rate at which pups were produced (46.8%). Differences in offspring survival only explained 12.2% of the variance in reproductive success of dominant males (Table 4).

Discussion

Our aim in this study was to investigate the factors that influence dominance acquisition in male meerkats, and the extent and causes of variation in reproductive success while dominant. The high degree of reproductive skew found is comparable to that of males in other highly cooperative breeders [e.g. in dwarf mongooses (*Helogale parvula*), the dominant male sires about 75% of offspring (Creel & Macdonald 1995); in African wild dogs (*Lycaon pictus*), the dominant male sires 80–90% (Creel & Creel 2002); and in the cooperatively breeding Florida scrub jay (*Aphelocoma coerulescens*), extra-pair fertilization is virtually absent, purportedly due to large territory size and low variation in the quality of territory-holding males (Quinn *et al.* 1999)]. Given the high reproductive skew among male meerkats, one might predict strong competition among

Table 3 Factors affecting the proportion of pups in the group sired by the dominant male (based on 106 litters)

Variable	Estimate	SE	d.f.	P value	Comments
No. of male competitors	-1.49	0.32	103	< 0.002	Only males unrelated to dominant female at conception
No. of prospectors	-0.56	0.18	103	0.003	At 2 weeks around the conception
Group size	0.76	0.29	103	0.01	At conception
Male age (days)	0.04	0.03	102	0.23	At conception
Male weight (g)	0.00	0.00	84	0.66	Mean weight during the 30 days preceding conception
Rainfall (mm)	0.00	0.00	90	0.40	Total rainfall during 3 months preceding conception
No. of females unrelated to DM in group	-0.12	0.34	102	0.73	At conception; DM, dominant male
Constant	3.48	1.01	103	< 0.001	

Results from a generalized linear model with a binomial error structure and logit link function. Group and individual were tested as random terms, but were nonsignificant and dropped from the analysis ($P > 0.05$).

Table 4 Analysis of variance components of reproductive success in dominant male meerkats

Component	Proportion of variance explained	B	SE	d.f.	Comment
Dominance tenure (reproductive lifespan)	41.0%	0.86	0.14	1,34	No. of months in tenure
Breeding rate	46.8%	0.98	0.14	1,34	No. of pups produced/month
Offspring survival	12.2%	0.25	0.17	1,34	Proportion of offspring surviving to 90 days
	100%				

Multiple regression of components affecting reproductive success. All variables were log-transformed to make the model additive (rather than multiplicative, which introduces interaction effects). Standardized regression coefficients (B) were used to derive the relative proportion of variance explained by each variable. The total number of offspring surviving to 90 days was used as the dependent variable. See Clutton-Brock (1988) for discussion on alternative methods on how to perform this analysis.

males to attain and retain the dominant position. We show that age strongly influenced the outcome of contests for dominance, but found no evidence that either dominance acquisition or tenure length were correlated to body weight, a trait often correlated to successful dominance. Instead, our results indicate that both the time spent in the dominant position and the proportion of offspring sired by the dominant male, both important components of male reproductive success, are strongly influenced by group size and composition.

Given the intense competition between male meerkats for dominant breeding positions, strong sexual selection on phenotypic traits associated with fighting abilities might be expected (e.g. large size or weaponry (Kruuk *et al.* 2002)). However, our analyses revealed that the relative weight of males had no apparent influence on the outcome of dominance contests, but instead that the relative age of males during contests for dominance was a strong predictor of the outcome. Age has been shown to have an important influence on the outcome of competition for dominance in other species, particularly in primates and other carnivores

(e.g. chimpanzees *Pan troglodytes*, Goodall 1986; dwarf mongooses, Creel *et al.* 1995). The importance of age may have several explanations. First, the correlation between age and the outcome of dominance struggles could be an effect of experience. For example, in a study of Weddell seals (*Leptonychotes weddellii*), another species with pronounced male-male competition and high male reproductive skew, previous mating experiences explained nearly 40% of the variation in male reproductive success, independent of age (Harcourt *et al.* 2007). Second, age may also affect the relative pay-offs for the contestants. Younger males, with most of their lifetime reproduction ahead of them may be unwilling to escalate fights as far as older males are willing to do. This is thought to explain why older male song sparrows defend their territories more vigorously than younger conspecifics, regardless of previous experience of the specific area (Hyman *et al.* 2004). In meerkats, such a mechanism would be further augmented by their carnivorous dentition, well adapted for fighting, since situations where both contestants have the capacity to inflict serious injuries to their opponent, small differences in relative pay-offs of winning a fight may more

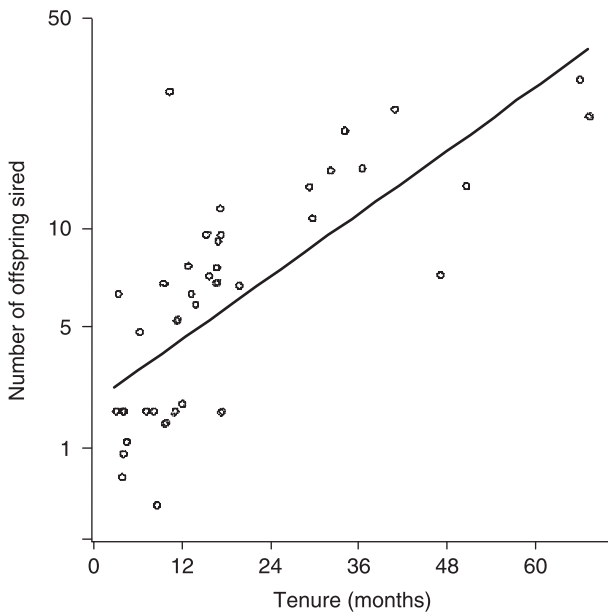


Fig. 4 Reproductive output of dominant males (with dominance periods > 90 days, $N = 40$). The figure plots the 'number of offspring sired' against 'tenure', while controlling for the proportion of offspring genotyped during the male's tenure. Note that the y -axis is logarithmic as the dependent variable in the model (number of offspring) had to be log-transformed for normality. We only included tenures exceeding 3 months (see Methods).

strongly bias the outcome than physical attributes. For example, the rarity of challenges in lions for the acquisition of mating partners or food items held by other individuals, even when considerable size differences exist between individuals, probably reflects the high costs of fighting in this species (Packer *et al.* 1991). A similar explanation has been invoked to explain the reproductive egalitarianism in many gallinule birds (Jamieson & Craig 1987). But why the relative weight of males (even between same-aged competitors) had no influence on the outcome of dominance contests awaits a definite answer.

Once dominant, variation in tenure length explains 41% of the variation in total reproductive success of males. As over 40% of males lost their dominance because either they or their partner died, stochastic events such as predation will clearly have an important influence on male tenure length. However, despite the importance of these chance events, our analyses revealed that social factors explained a significant amount of variation in tenure length. Dominant males in larger groups had longer tenures, whereas those in groups with more females experienced shorter tenures. While there has been little investigation of the factors affecting dominance tenure in cooperatively breeding species, there is some evidence from noncooperative species that group size and composition influence tenure length. For example, in mandrills (*Mandrillus sphinx*), alpha male

tenure declined with the number of mature and adolescent male rivals in the group (Setchell *et al.* 2006), and in lions (Packer *et al.* 1988) and Thomas' langurs *Presbytis thomasi* (Steenbeek 2000), male tenure was shorter in groups containing large numbers of females. The increased tenure length of dominant male meerkats in larger groups may arise because larger groups are better able to ward off approaches from prospecting males who might otherwise take over the group and displace the resident dominant. Alternatively, this correlation could be a consequence of group size effects on survival. Individuals in larger groups show higher survival (Clutton-Brock *et al.* 1999a), and hence hold tenure for longer. Finally, this correlation could reflect in part the fact that many tenures start when new groups are founded, and so as tenure length increases, groups might be expected to be larger, as newly founded groups tend to grow in size over time. The causes of the negative correlation between tenure length and female number is less clear, but perhaps groups with a large number of females attract the attention of other males, so that dominant males in such groups are challenged more frequently, both by subordinates immigrants within the group and by prospecting males from other groups. The general importance of tenure for reproductive success has been shown in a number of species [e.g. lions (Packer *et al.* 2001); hyenas *Crocuta crocuta* (East & Hofer 2001; Engh *et al.* 2002)].

Variation in breeding rates explains a further 47% of variation in male reproductive success. Because the dominant female accounts for about 90% of the total offspring production, the dominant male breeding rate is to a large extent governed by the product of the reproductive rate of the dominant female and the dominant male's ability to capitalize the reproductive share of these litters. The rate of litter production by the dominant female has been explored in previous work and is known to depend on the dominant female's phenotype (e.g. age and weight) as well as group size and composition (Russell *et al.* 2003; Hodge *et al.* 2008). We show that, in males, group size also influences the proportion of the dominant females' offspring that the dominant male sires. Dominant males sire a greater proportion of pups in large groups, again perhaps because larger groups are better able to ward off extra-group males. However, the proportion of offspring sired by the dominant also decreases as the number of competitors increases, declining with both the number of adult males within the group, as well as the number of prospecting males approaching from other groups. Dominant males guard the dominant female vigorously when she is in estrus, which probably helps to reduce these losses in paternity. Positive effects on paternity certainty from pre- and post-copulatory mate guarding are known from many other systems (e.g. Gullberg *et al.* 1997; Schleicher *et al.* 1997; Komdeur 2001), although the effectiveness of mate guarding varies widely between systems. For example, in mountain

gorillas (*Gorilla beringei beringei*) dominant males lose about 15% of paternity to subordinate males (Bradley *et al.* 2005) while in many bird species, extra-pair paternity can reach 76% despite territoriality and mate guarding (Griffith *et al.* 2002). In meerkats, mate guarding by the dominant male is facilitated by diurnal foraging in open habitats, the use of sleeping burrows during the night (where individuals are likely to remain in close proximity to conserve heat) and group territoriality (extra-group males are attacked when approaching the group), which may help to explain the relatively low rates of extra-pair paternity observed in this species. The apparent payoffs from ardent mate-guarding are likely to explain why dominant males never leave the group on prospecting forays or contribute to babysitting (Clutton-Brock *et al.* 2004), since this would leave the dominant female unattended.

In addition to male mate guarding, female choice may also help to explain why skew is high among males and extra-pair paternity is relatively low. Inbreeding avoidance by the dominant female prevents many of the natal males from reproducing within the group, and the xenophobic behaviour of group males towards other males limits the dominant female's immediate choice of mating partners. The dominant female may also prefer to mate with the dominant male, as dominants are successful dispersers and successful contestants, and have therefore proven their high quality. The potential genetic rewards of mating with other males may be limited, and the incentive for females to seek mating opportunities elsewhere may thus be low, as has been suggested for some cooperative bird species showing strong mate fidelity (Quinn *et al.* 1999; Magrath *et al.* 2004).

In summary, the reproductive success of male meerkats largely depends on whether they attain the dominant position during their lifetime, and once dominant, on their tenure and reproductive rate. Our results indicate that social factors are of primary importance, influencing both the time that males spend in the dominant position as well as the number of offspring that they sire. Males in large groups hold the dominant position for longer and are cuckolded less. However, their breeding success depends not only upon the size of the group, but also upon its composition, as dominant males had shorter tenures and sired fewer offspring when the number of competitors within the group was high. These findings highlight the importance of considering group composition, as well as group size, when investigating the factors that influence dominant breeding success in social species. Few studies of cooperative species have been able to investigate the factors that influence the reproductive success of dominant male breeders, and as such, our findings improve our understanding of the selective pressures that operate among males in such societies. Further research into the relative importance of individual traits and social factors in determining the

reproductive success of males in other cooperative species is now needed.

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References

- Amos W, Wilmer JW, Fullard K *et al.* (2001) The influence of parental relatedness on reproductive success. *Proceedings of the Royal Society B: Biological Sciences*, **268**, 2021–2027.
- Bensch S, Hasselquist D, Nielsen B, Hansson B (1998) Higher fitness for philopatric than for immigrant males in a semi-isolated population of great reed warblers. *Evolution*, **52**, 877–883.
- Blums P, Clark RG (2004) Correlates of lifetime reproductive success in three species of European ducks. *Oecologia*, **140**, 61–67.
- Bradley BJ, Robbins MM, Williamson EA *et al.* (2005) Mountain gorilla tug-of-war: silverbacks have limited control over reproduction in multimale groups. *Proceedings of the National Academy of Sciences, USA*, **102**, 9418–9423.
- Brommer JE, Merila J, Kokko H (2002) Reproductive timing and individual fitness. *Ecology Letters*, **5**, 802–810.
- Cant MA, Reeve HK (2002) Female control of the distribution of paternity in cooperative breeders. *American Naturalist*, **160**, 602–611.
- Chesser RK (1991) Gene diversity and female philopatry. *Genetics*, **127**, 437–447.
- Clutton-Brock T (1988) *Reproductive Success*. University of Chicago, Chicago.
- Clutton-Brock TH (1998a) Introduction: studying reproductive costs. *Oikos*, **83**, 421–423.
- Clutton-Brock TH (1998b) Reproductive skew, concessions and limited control. *Trends in Ecology & Evolution*, **13**, 288–292.
- Clutton-Brock TH, Gaynor D, McIlrath GM *et al.* (1999a) Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. *Journal of Animal Ecology*, **68**, 672–683.
- Clutton-Brock TH, Maccoll A, Chadwick P *et al.* (1999b) Reproduction and survival of suricates (*Suricata suricatta*) in the southern Kalahari. *African Journal of Ecology*, **37**, 69–80.
- Clutton-Brock TH, Brotherton PNM, O'Riain MJ *et al.* (2001a) Contributions to cooperative rearing in meerkats. *Animal Behaviour*, **61**, 705–710.
- Clutton-Brock TH, Brotherton PNM, Russell AF *et al.* (2001b) Cooperation, control, and concession in meerkat groups. *Science*, **291**, 478–481.
- Clutton-Brock TH, Russell AF, Sharpe LL (2003) Meerkat helpers do not specialize in particular activities. *Animal Behaviour*, **66**, 531–540.
- Clutton-Brock TH, Russell AF, Sharpe LL (2004) Behavioural tactics of breeders in cooperative meerkats. *Animal Behaviour*, **68**, 1029–1040.
- Creel S, Creel NM (2002) *The African Wild Dog: Behavior, Ecology, and Conservation*. Princeton University Press, Princeton, New Jersey.

- Creel S, Macdonald D (1995) Sociality, group-size, and reproductive suppression among carnivores. *Advances in the Study of Behavior*, **24**, 203–257.
- Creel S, Monfort SL, Creel NM, Wildt DE, Waser PM (1995) Pregnancy, estrogens and future reproductive success in Serengeti dwarf mongooses. *Animal Behaviour*, **50**, 1132–1135.
- Dobson FS, Chesser RK, Hoogland JL, Sugg DW, Foltz DW (1998) Breeding groups and gene dynamics in a socially structured population of prairie dogs. *Journal of Mammalogy*, **79**, 671–680.
- East ML, Hofer H (2001) Male spotted hyenas (*Crocuta crocuta*) queue for status in social groups dominated by females. *Behavioral Ecology*, **12**, 558–568.
- Engh AL, Funk SM, Van Horn RC *et al.* (2002) Reproductive skew among males in a female-dominated mammalian society. *Behavioral Ecology*, **13**, 193–200.
- Faulkes CG, Bennett NC, Bruford MW *et al.* (1997) Ecological constraints drive social evolution in the African mole-rats. *Proceedings of the Royal Society B: Biological Sciences*, **264**, 1619–1627.
- Field J, Solis CR, Queller DC, Strassmann JE (1998) Social and genetic structure of paper wasp cofoundress associations: Tests of reproductive skew models. *American Naturalist*, **151**, 545–563.
- Goodall J (1986) *The Chimpanzees of Gombe*. Belknap Press, Cambridge, Massachusetts.
- Goodman SJ (1997) Dinucleotide repeat polymorphisms at seven anonymous microsatellite loci cloned from the European harbour seal (*Phoca vitulina vitulina*). *Animal Genetics*, **28**, 310–311.
- Goodnight KF, Queller DC (1999) Computer software for performing likelihood tests of pedigree relationships using genetic markers. *Molecular Ecology*, **8**, 1231–1234.
- Griffin A, Nurmberger B, Pemberton JM (2001) A panel of microsatellite markers developed for meerkats (*Suricata suricatta*) by cross-species amplification and species-specific cloning. *Molecular Ecology Notes*, **1**, 83–85.
- Griffin AS, Pemberton JM, Brotherton PNM *et al.* (2003) A genetic analysis of breeding success in the cooperative meerkat (*Suricata suricatta*). *Behavioral Ecology*, **14**, 472–480.
- Griffith SC, Owen IPF, Thuman KA (2002) Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Molecular Ecology*, **11**, 2195–2212.
- Gullberg A, Olsson M, Tegelstrom H (1997) Male mating success, reproductive success and multiple paternity in a natural population of sand lizards: Behavioural and molecular genetics data. *Molecular Ecology*, **6**, 105–112.
- Harcourt RG, Kingston JJ, Cameron MF, Waas JR, Hindell MA (2007) Paternity analysis shows experience, not age, enhances mating success in an aquatically mating pinniped, the Weddell seal (*Leptonychotes weddellii*). *Behavioral Ecology and Sociobiology*, **61**, 643–652.
- Haydock J, Koenig WD (2003) Patterns of reproductive skew in the polygynandrous acorn woodpecker. *American Naturalist*, **162**, 277–289.
- Heinsohn R, Legge S (2003) Breeding biology of the reverse-dichromatic, co-operative parrot *Ecliptus roratus*. *Journal of Zoology*, **259**, 197–208.
- Hodge SJ, Manica A, Flower TP, Clutton-Brock TH (2008) Determinants of reproductive success in dominant female meerkats. *Journal of Animal Ecology*, **77** (1), 92–102.
- Holmes NG, Dickens HF, Parker HL *et al.* (1995) 18 canine microsatellites. *Animal Genetics*, **26**, 132–133.
- Hood GM (2004) POPTOOLS version 2.6.2. www.csc.csiro.au/poptools
- Hyman J, Hughes M, Searcy WA, Nowicki S (2004) Individual variation in the strength of territory defense in male song sparrows: Correlates of age, territory tenure, and neighbor aggressiveness. *Behaviour*, **141**, 15–27.
- Jamieson IG, Craig JL (1987) Dominance and mating in a communal polygynandrous bird – cooperation or indifference towards mating competitors. *Ethology*, **75**, 317–327.
- Jensen H, Saether BE, Ringsby TH *et al.* (2004) Lifetime reproductive success in relation to morphology in the house sparrow *Passer domesticus*. *Journal of Animal Ecology*, **73**, 599–611.
- Koenig WD, Dickinson JL (2004) *Ecology and Evolution of Cooperative Breeding in Birds*. Cambridge University Press, Cambridge, UK.
- Komdeur J (2001) Mate guarding in the Seychelles warbler is energetically costly and adjusted to paternity risk. *Proceedings of the Royal Society of London B: Biological Sciences*, **268**, 2103–2111.
- Kruuk LEB, Slate J, Pemberton JM *et al.* (2002) Antler size in red deer: heritability and selection but no evolution. *Evolution*, **56**, 1683–1695.
- Lucas JR, Waser P, Creel S (1994) Death and disappearance: estimating mortality risks associated with philopatry and dispersal. *Behavioral Ecology*, **5**, 135–141.
- Magrath RD, Johnstone RA, Heinsohn RG (2004) Reproductive skew. In: *Ecology and Evolution of Cooperative Breeding in Birds* (eds Koenig WD, Dickinson JL). Cambridge University Press, Cambridge, UK.
- Maniatis T, Fritsch EF, Sambrook J (1982) *Molecular Cloning. A Laboratory Manual*. Cold Spring Harbor Press, Cold Spring Harbor, New York.
- Marshall TC (2001). CERVUS. University of Edinburgh, Edinburgh, UK.
- Menotti-Raymond M, David VA, Lyons LA *et al.* (1999) A genetic linkage map of microsatellites in the domestic cat (*Felis catus*). *Genomics*, **57**, 9–23.
- O’Riain MJ, Bennett NC, Brotherton PNM, McIlrath G, Clutton-Brock TH (2000) Reproductive suppression and inbreeding avoidance in wild populations of co-operatively breeding meerkats (*Suricata suricatta*). *Behavioral Ecology and Sociobiology*, **48**, 471–477.
- Packer C, Pusey A (1993) Dispersal, kinship and inbreeding in African lions. In: *The Natural History of Inbreeding and Outbreeding* (ed. Thornhill, NW), pp. 375–391. University of Chicago Press, Chicago.
- Packer C, Gilbert DA, Pusey AE, Obrien SJ (1991) A molecular genetic-analysis of kinship and cooperation in African lions. *Nature*, **351**, 562–565.
- Packer C, Herbst L, Pusey AE *et al.* (1988) Reproductive success of lions. In: *Reproductive Success* (ed. Clutton-Brock TH). Chicago University Press, Chicago.
- Packer C, Pusey AE, Eberly LE (2001) Egalitarianism in female African lions. *Science*, **293**, 690–693.
- Pinheiro JC, Bates DM (1996) Unconstrained parameterizations for variance-covariance matrices. *Statistics and Computing*, **6**, 289–296.
- Quinn JS, Woolfenden GE, Fitzpatrick JW, White BN (1999) Multi-locus DNA fingerprinting supports genetic monogamy in Florida scrub-jays. *Behavioral Ecology and Sociobiology*, **45**, 1–10.
- Raymond M, Rousset F (1995) GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. *Journal of Heredity*, **86**, 248–249.
- Reeve HK, Emlen ST, Keller L (1998) Reproductive sharing in animal societies: reproductive incentives or incomplete control by dominant breeders? *Behavioral Ecology*, **9**, 267–278.
- Russell AF, Clutton-Brock TH, Brotherton PNM *et al.* (2002) Factors affecting pup growth and survival in cooperatively breed-

- ing meerkats *Suricata suricatta*. *Journal of Animal Ecology*, **71**, 700–709.
- Russell AF, Brotherton PNM, McIlrath GM, Sharpe LL, Clutton-Brock TH (2003) Breeding success in cooperative meerkats: effects of helper number and maternal state. *Behavioral Ecology*, **14**, 486–492.
- Schleicher B, Hoi H, Valera F, Hoi Leitner M (1997) The importance of different paternity guards in the polygynandrous penduline tit (*Remiz pendulinus*). *Behaviour*, **134**, 941–959.
- Setchell JM, Wickings EJ, Knapp LA (2006) Life history in male mandrills (*Mandrillus sphinx*): physical development, dominance rank and group association. *American Journal of Physical Anthropology*, **131**, 498–510.
- Solomon NG, French JA (1997) *Cooperative Breeding in Mammals*. Cambridge University Press, Cambridge, UK.
- StatSoft I (2005) STATISTICA (data analysis software system). Version 7.1. www.statsoft.com.
- Steenbeek R (2000) Infanticide by males and female choice in Thomas' langurs. In: *Infanticide by Males and its Implications* (eds van Schaik CP, Janson CH). Cambridge University Press, Cambridge, UK.
- Vehrencamp SL (1983) A model for the evolution of despotic versus egalitarian societies. *Animal Behaviour*, **31**, 667–682.
- VSN-International (2005) GENSTAT. Lawes Agricultural Trust. www.vsn.co.uk.
- Young AJ, Clutton-Brock TH (2006) Infanticide by subordinates influences reproductive sharing in cooperatively breeding meerkats. *Biology Letters*, **2**, 385–387.
- Young AJ, Carlson AA, Clutton-Brock T (2005) Trade-offs between extraterritorial prospecting and helping in a cooperative mammal. *Animal Behaviour*, **70**, 829–837.
- Young AJ, Carlson AA, Monfort SL *et al.* (2006) Stress and the suppression of subordinate reproduction in cooperatively breeding meerkats. *Proceedings of the National Academy of Sciences, USA*, **103**, 12005–12010.
- Young AJ, Spong G, Clutton-Brock TH (2007) Helper males prospect for extra-group matings: alternative reproductive tactics in a cooperative mammal. *Proceedings of the Royal Society of London B: Biological Sciences*, **274**, 1603–1609.

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